Growth Effects of Mineral Nutrients Applied to the Substrate or onto the Leaves in Four Carnivorous Plant Species

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The majority of terrestrial carnivorous plants (CPs) grow on mineral poor and wet soils. Moreover, another common characteristic of carnivorous plants is the weakly developed root system. The limited capacity for mineral nutrient uptake by roots of CPs may be partially compensated by the absorption of nutrients from the caught prey. The question of the relative contributions of roots and trapping leaves to the nutrient supply necessary to normal growth has long been considered. Now, it is accepted that no CP can sustain its growth when fed only with insects as prey via leaves (Juniper et al., 1989, p. 130). However, normal growth and development of CPs can take place even when no feeding with insects is applied. Juniper et. al. (1989, p. 130-134) reviewed in their recent monograph the results concerning the growth effects of mineral nutrients added to root substrate (solution) or feeding with small animals on the leaves of CPs. Feeding with insects on the leaves always led to an appreciable enhancement of growth in greenhouse cultivation in various species of CPs grown in mineral poor media. This finding has recently been confirmed also in natural populations of *Drosera intermedia* and *D. rotundifolia* (Thum, 1988).

Feeding the CPs with insect bodies is not the only way of feeding and it may be successfully replaced by adding small pieces of agar gel impregnated with nutrient solution on the trapping parts of leaves (Karlsson & Carlsson, 1984). The authors found that it was mainly phosphate added as agar gel droplets on the leaves that enhanced appreciable growth in the common butterwort, *Pinguicula vulgaris*, and led to an increase of total amount of both phosphorus and nitrogen in plants. It is remarkable that the increase of the total phosphorus absorbed by the P-fertilized plants, as compared with controls, was about 1.5-2.5 times higher than the dose added on the leaves. The same phenomenon was observed also for nitrogen in the same species when the plants were fed with small flies (ratio of 1.6; Aldenius et al., 1983). These results suggest that the leaf uptake of phosphate (and perhaps also of other nutrients) stimulates the effective uptake of many mineral nutrients by roots.

Many CPs are able to enhance markedly their growth and nutrient content in tissues after mineral nutrients have been added to a nutrient-poor substrate (or solution; for review see Juniper et al., 1989, p. 130-134). However, negative interactions between feeding with insects on leaves and nutrient uptake by roots also takes place in CPs and they reduce the growth and total nutrient content in plants (Chandler & Anderson, 1976). In any case, the uptake capacity of roots for mineral nutrients from soil is relatively low in CPs. Moreover, when the roots of CPs were grown in nutrient-rich soils, growth was significantly reduced and the plants lost some features of carnivory (Roberts & Oosting, 1958; Eleuterius & Jones, 1969). Thus, mineral nutrients may be added only with caution to the substrates for cultivation of CPs. The

above fact that the growth of CPs may be considerably enhanced by moderate mineral fertilization both of substrates and on trapping leaves might have a practical application in the cultivation of CPs. In this paper, we compare the growth effects of mineral nutrients added either to a peaty substrate or on trapping parts of leaves as well as the effect of substrate alkalization in four species of CPs. The effectiveness of utilization of added nutrients in plants is discussed.

Four species of CPs were used for experimental cultivation: *Drosera adelae* F. Muell., *D. aliciae* Hamet, *D. capillaris* Poir., and *Dionaea muscipula* Ell. These species originate from various continents. They are often cultivated by growers. An acid fen soil (l kg of fresh weight, FW) with washed sand (0.5 l) was used as a substrate in all experimental variants. The fen soil was obtained from an acid fen near Trebon town (Trebon Biosphere Reserve, South Bohemia, Czechoslovakia). It originated from the litter of sedges and common reed overgrown by a wet needle-leaf forest. It was of brown-black color, with short filaments.

Some basic analyses of the fen soil were performed. Data are available to show that the content of accessible (exchangeable) Ca, Mg, Na, K, and Fe in the fen soil was sufficient to support plant growth. Dry weight, DW, (105 °C for 3 hours) amounted to 24.9% of FW. One gram of the fen soil (FW) was shaken with 5 ml of distilled water; the pH was in average 3.97, rather low for a fen soil, and it dropped to 3.35 after adding KCl (exchange pH value) indicating a high cation-exchange capacity. Electrical conductivity of the soil suspension was rather low (47 $\mu S.cm^{-1}$) indicating that the fen soil was nutrient-poor. Thus, the fen soil pH was about 4.0 in all but one variant.

In one variant.the fen soil was alkalized by means of $NaHC0_3$ to a pH of about 5.2 prior to cultivation. Titration of the fen soil suspension with 0.1 $mol.l^{-1}$ $NaHC0_3$ revealed that its buffering (and/or neutralization) capacity was very high. To reach pH 5.2, it was necessary to add 21.5 mmol (1.81 g) $NaHC0_3$ to 1 kg (FW) of the fen soil (i.e., 86 mmol per kg of DW. We also estimated how easily the acid fen soil could be neutralized by $HC0_3^-$ from the tap water which was used for watering in all variants. We found that, owing to the high buffering capacity of the soil, as much as 50 ml of tap water might be added to 1 g of the fen soil (FW) for pH to rise by only 1.0 unit (from 4.0 to 5.0). The $HC0_3^-$ concentration of the tap water used was about 0.7 $mmol.l^{-1}$ (42 $mg.l^{-1}$), its pH 7.2-7.5, and electrical conductivity about 76 $\mu S.cm^{-1}$. The mean $N0_3^-$ concentration in the tap water was about 3 $mg.l^{-1}$ (i.e., about 0.7 $mg.l^{-1}$ of N03-N); other N salts were not present. Phosphate concentration was extremely low, within 3-5 $\mu g.l^{-1}$ of $HP0_4$-P. The mean Ca^{2+} concentration was about 25 $mg.l^{-1}$. K^+, Na+, Mg2+, and $S0_4^{2-}$ ions were also present in low concentrations.

On 16 February 1990, ten small plants of each of the four species were planted together on the fen soil with sand (see above) in each of four glass aquaria (18 x 20 x 20 cm); 0.25 kg DW of the fen soil was present in all of them. The substrate depth was about 5.5 cm. Uniform seedlings of *D. aliciae* and *D. capillaris*, plantlets of *Dionaea* from meristem tissue culture, and *D. adelae* plantlets arising from root regeneration buds were used. The aquaria with plants, covered by pieces of glass, were placed on a window ledge of SW orientation. Tap water was added to keep the water table at about a half of the substrate depth. Over the whole cultivation period, 2.5-3.0 l of tap water was added to each aquarium. The temperature inside the aquaria ranged from 18 to 27 °C. In summer, the aquaria were shaded by thin paper sheets preventing them from overheating. the position of individual aquaria on the window ledge was rotated regularly at one-week intervals.

Variants of mineral nutrition

Each aquarium with 10 plants of each of the four CP species represented one variant. The variants were as follows:

1. Control, denoted as "C". The substrate was watered with tap water only.
2. Variant whose substrate was alkalized to pH of about 5.2 (see above) by adding $NaHCO_3$ prior to experiment. It is denoted as "ALK". The substrate pH dropped during the experiment and was reset at pH 5.2 by further additions of $NaHCO_3$.
3. Variant (denoted as "NS-S") whose substrate was homogeneously fertilized by 50 ml of mineral nutrient solution of the following composition: (in mg.l-1): NH_4NO_3 200.1, KH_2PO_4 100.7, $MgSO_4 \cdot 7H2O$ 101.1, $CaCl_2$ 110.0, $FeCl_3$ 2.6. Thus, the mean nutrient concentration in the substrate rose by (in mg of element·kg^{-1} DW): N 14.0; P 4.6;, K 5.8; S 2.6; Ca 8.0; Mg 2.0; Cl 17.6; Fe 0.18.
4. Variant (denoted as "NS-L") where the same mineral nutrient solution as in NS-S was dropped on trapping parts of the leaves once a week. A droplet of 1 or 2 µl was applied on either one or two of the leaves of each plant. Thus, the total volume of the nutrient solution per plant amounted to 92 µl in *D. adelae*, 38 µl in *D. aliciae*, 92 µl in *D. capillaris*, and 46 µl in *Dionaea* during the whole cultivation.

On 3 March 1990, 15 days after planting, the length of the longest leaf was measured in all plants. This date is considered to be the onset of proper cultivation as plants could be injured during planting. The leaf length was measured also on 16 May, 20 June, and 6 October. The cultivation was finished on 6 October, 217 days after the date of the first leaf measurement. The length of the longest root was measured in all plants. Both roots and shoots of 10 plants of each variant were dried (105 C for 3 hrs) and weighed. The dead biomass was not separated. It was negligible in all *Drosera* plants but it could amount to some 30% of the *Dionaea* shoot weight and even 40-50% in the NS-L variant. The leaf and root lengths were always expressed as mean value ±2.SEM.

The results (Figs. 1-4; Table I) show that all control plants (C) grew rather slowly. The length of the longest leaf or root may be understood only as a rough measure since it did not reflect the total plant biomass too closely and, moreover, it had a high variance. Except for *D. capillaris*, no distinct increase of plant biomass took place in the alkalized substrate (ALK). In all *Drosera* species, when supplied with mineral nutrients either to the substrate (NS-S) or on the leaves (NS-L), their shoot and root growth was markedly promoted and their total biomass rose to about 2.4 to 17 times that in controls. The vigorous growth of *Drosera* shoots more closely correlated with root growth although the shoot/root ratio (dry weight) was appreciably higher than in controls only in NS-L. *Dionaea,* however, did not react positively to nutrient supply applied either to roots or on leaves. In the latter case, the extremely high ratio of dead biomass was probably due to frequent closing of the leaf traps.

A remarkable phenomenon was observed in all *Drosera* species in the NS-L variant. The amount of mineral nutrients in the total plant biomass minus the nutrient amount in the controls was many times higher than that added on the leaves as nutrient solution during the whole experiment (Table II). Published data on the mean nutrient content in dry biomass of *Drosera* were drawn from Juniper et al. (1989; Tab. 11.1, p. 230) and Dykyjová & Drbal (1984; Tab. 3, p. 82). The following values were used (in mg of element.g^{-1} DW): N 11; P 1.25; K 11; Ca l; Mg 1.95; Fe 0.5. Similarly, the increase of total plant biomass in the NS-S variant theoretically was higher (against the controls) than would be expected from the nutrient supply to substrate (for N about 1.4 times~ K 3.4, and Mg 1.8 times).

The present results support fully the literature data in that the growth of CPs can be promoted appreciably by mineral nutrient supply either to the substrate or directly on the leaves (cf. Juniper et al., 1989, p. 130-134). This finding is of a very practical importance for all growers of CPs as it is very easy and cheap to add a mineral nutrient solution to substrate or spray the leaves of CPs with the same solution. The sprayed nutrients that fall on the substrate can be taken up by roots. The greatest advantage

Table I. Results of growth experiment after 217 days of cultivation. Variants: C, controls; ALK, substrate alkalization; NS-S, nutrient solution added to substrate, NS-L, nutrient solution dropped on leaves. Length of the longest root was measured in 10 plants. DW, dry weight.

Variants	Root length ±2.SEM (cm)	Shoot DW (mg)	Root DW	Shoot DW / Root DW
A. Drosera Adelae				
C	4.1 ± 1.2	15.1	4.5	3.3
ALK	3.0 ± 2.3	7.7	2.9	2.7
NS-S	10.6 ± 3.2	43.0	13.0	3.3
NS-L	8.1 ± 1.9	38.4	8.9	4.3
B. Drosera aliciae				
C	0.52 ± 0.11	0.24	0.04	6.0
ALK	0.65 ± 0.20	0.31	0.06	5.2
NS-S	3.6 ± 0.6	4.3	0.62	6.9
NS-L	1.3 ± 0.6	3.1	0.14	21.9
C. Drosera capillaris				
C	2.7 ± 1.1	4.7	0.70	6.7
ALK	2.3 ± 0.5	8.3	0.76	11.0
NS-S	7.3 ± 2.6	15.3	2.3	6.6
NS-L	6.5 ± 2.7	19.9	2.4	8.4
D. Dionaea muscipula				
C	3.0 ± 1.3	27.5	0.96	28.7
ALK	2.0 ± 0.7	14.0	0.65	21.5
NS-S	3.2 ± 1.0	19.7	0.63	31.3
NS-L	3.5 ± 1.5	28.3	0.89	31.8

Table II. The theoretical increase of the total nutrient content in the NS-L variant as compared with controls divided by the total nutrient content dropped on the leaves (i.e., the effectiveness o utilization of the nutrient added).

Species	N	P	K	Ca	Mg	Fe
D. adelae	47.2	16.4	114.	7.5	58.8	169
D. aliciae	12.1	4.2	29.2	1.9	15.0	43.2
D. capillaris	28.9	10.1	70.0	4.6	36.0	103

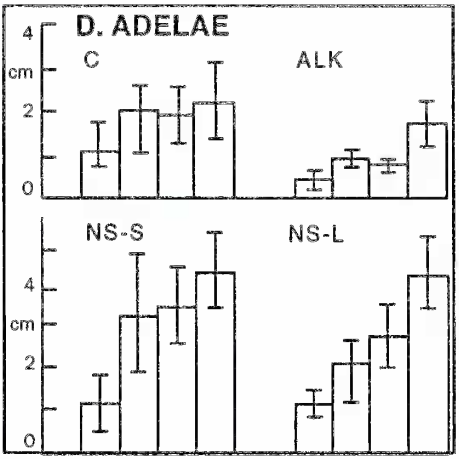

Figure 1

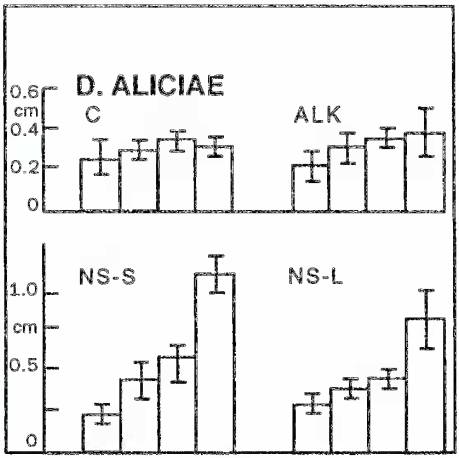

Figure 2

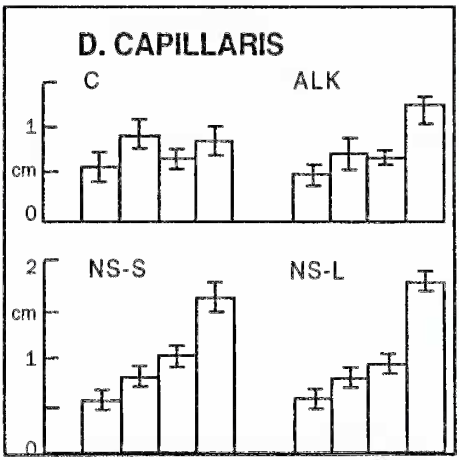

Figure 3

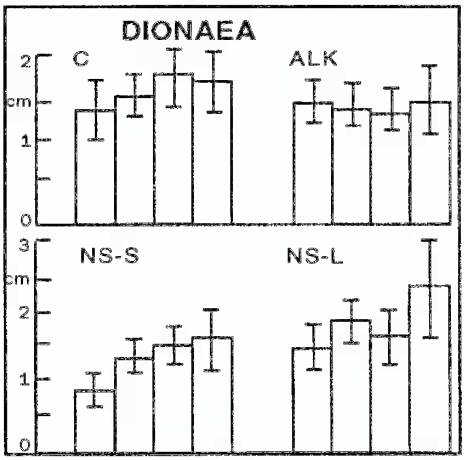

Figure 4

Legends to the figures:

Figure 1. The mean length of the longest leaf in *D. adelae* in the course of 217-day cultivation ±2.SEM; n=10. Variants: C=controls, ALK=substrate alkalization, NS—S=nutrient solution to the substrate, NS-L=nutrient solution dropped on the leaves. Date of measurements from left to right in tetrad of columns: 3 MAR, 16 MAY, 20 JUN, 6 OCT.

Figure 2. The mean length of the longest leaf in *D. aliciae*. For explanation see Figure 1.

Figure 3. The mean length of the longest leaf in *D. capillaris*. For explanation, see Figure 1.

Figure 4. The mean length of the longest leaf in *Dionaea muscipula*. For explanation, see Figure 1.

of a mineral nutrient solution is that it cannot get mouldy. However~ it is necessary to take into account that overfertilization of a substrate can lead to reduction of growth (Roberts & Oosting, 1958; Eleuterius & Jones, 1969). There was a relatively low growth rate in all plants during our experiment, probably due to low light intensity. Thus, it is reasonable to suppose that if the external growth conditions had been optimal, the growth effects of added nutrients would have been even more distinct. *Dionaea* however, seems to be adapted to a very low nutrient content in the soil and also its capacity to absorb mineral nutrients by leaves is negligible.

The aim of substrate alkalization was to find out whether the growth of CPs might be promoted by a pH higher than that in a natural acid fen soil. Except for *D. capillaris*, ecologically a very resistant species, alkalization resulted in the same or reduced growth (Figs. 1-4; Table I). Similarly, Rychnovská-Soudková (1953, 1954) found the optimal growth of *Drosera rotundifolia* to be in a diluted nutrient solution at pH as low as 3.0. The very low pH protected the plants from a high Ca^{2+} concentration in the solution and NO_3^- was used efficiently as a source of N. At pH above 5.0 the growth was promoted significantly by NH_4^+ whereas Ca^{2+} and NO_3^- inhibited it. In general, it may be concluded that *Drosera* plants are more susceptible to elevated concentration of nutrients at higher pH values.

As Table II shows, the growth of the three *Drosera* species in the NS-L variant was so vigorous, compared to the controls, that the amount of major nutrients theoretically accumulated in the biomass was many times higher (for N, P, K, 4 to 114 times) than could be absorbed from the nutrient solution dropped on the leaves. However, the numerical data in Table II represent only rough estimates (approximate values) of the true ones as literature data on the nutrient content in *Drosera* species were used instead of analyses. Except for iron, the content of other elements was not too variable. Thus, it is reasonable to assume that the true nutrient content in biomass did not differ from that used for calculation more than by ±50%. i.e., the data in Table II lie also within this range. The nutrient content per biomass unit of CPs which were supplied with mineral nutrients or insects was not too different from that of controls and the former was usually somewhat higher (Chandler & Anderson, 1976; Aldenius et al., 1983; Karlsson & Carlsson, 1984). Therefore, the data shown in Table II could represent conservative estimates.

How can this intriguing phenomenon be explained? It is quite clear that the CPs in the NS-L variant absorbed the whole remaining amount of nutrients by roots from the fen substrate. Though chemical analysis of the fen soil used is lacking, it may be deduced from analyses of other similar fen soils of the Trebon basin (Dykyjová & Drbal, 1984) that the content of all nutrients in the fen soil used was high enough to ensure the observed increase of biomass. Moreover, small amounts of nutrients were introduced into the substrate in the tap water. Now, the question arises how dropping small amounts of nutrients on the leaves could cause the roots in the NS-L variant to take up so much nutrient from the relatively poor substrate? Two independent mechanisms may be suggested; they might also operate simultaneously. a) The supply of nutrients on the leaves of relatively small plants in the early phases of experiment could lead to a partial promotion of root growth. The longer roots would be capable of absorbing more nutrients from the poor substrate thus supporting more shoot growth. In the course of time, this positive feed-back mechanism could produce roots which were about 2-2.5 times longer than those of controls (Table I). Considering the three-dimensional distribution of these roots in the substrate, they could theoretically come in contact with about 8-15 times greater substrate volume than the controls. Probably, it could not be sufficient (cf. Table II). b) As stated by Aldenius et al. (1983) and Karlsson & Carlsson (1984) who also found this phenomenon for N and P, the leaf nutrient supply might result in an increased efficiency of nutrient uptake by roots from the substrate.

The latter authors concluded that the main candidate for the stimulation of nutrient uptake by roots of CPs was probably phosphate that had been absorbed by leaves. This conclusion was based mainly on the fact that the leaf uptake of phosphate itself led to a significant increase in the total N content of the plants. However, the leaf uptake of N and microelements interacted positively with that of P indicating that the stimulation of nutrient uptake by roots was more complex.

The same explanation may hold also for the NS-S variant. As all CPs in our experiment were grown in very humid air, the effect of dropping the nutrient solution on the leaves cannot be explained in terms of an increase in the supply of water itself.

Acknowledgment

The authors are indebted to Dr. Miloslav Studnicka, Head of the Botanical Garden in Liberec, Czechoslovakia, for his providing the experimental plants and valuable comments. Sincere thanks are due to Dr. Laurie E. Friday, University of Cambridge, U.K., for language correction of the manuscript and for helpful criticism.

References

Aldenius J., Carlsson B., Earlsson S., 1983. Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. New Phytol. 93: 53-59.

Chandler G.E., Anderson J.W., 1976. Studies on the nutrition and growth of *Drosera* species with reference to the carnivorous habit. New Phytol. 76: 129-141.

Dykyjová D., Drbal K., 1984. (Chemical composition of peat bog and acid fen vegetation in the Trebon basin.) In Czech. Preslia (Prague) 56: 73-91.

Eleuterius L.N., Jones S.B., 1969. A floristic and ecological study of pitcher plant bogs in south Mississippi. Rhodora 71: 29-34.

Juniper B.R., Robins R.J., Joel D.M,, 1989. Carnivorous Plants. Pp. 353, Academic Press Ltd, London.

Karlsson P.S., Carlsson B., 1984. Why does *Pinguicula vulgaris* trap insects? New Phytol. 97: 25-30.

Roberts P.R., Oosting H.J., 1958. Responses of Venus fly trap (*Dionaea muscipula*) to factors involved in its endemism. Ecol. Monographs 28: 193-218.

Rychnovská-Soudková M., 1953. Study on mineral nutrition of *Drosera rotundifolia* L. I. Influence of calcium as an important physiological and ecological factor. In Czech. Preslia (Prague) 25: 51-66.

Rychnovská-Soudková M., 1954. Study on mineral nutrition of *Drosera rotundifolia* L. II. Root sorption of inorganic nitrogen. In Czech. Preslia (Prague) 26: 55-66.

Thum M., 1988. The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary feeding. Oecologia 75: 472-480.

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